Evidence for Diel Horizontal Migration (DHM) of Crustacean Zooplankton In the Western Basin of Lake Erie

Senior Honors Thesis

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by

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ABSTRACT

1. Diel horizontal migration (DHM) has been observed in zooplankton in shallow lakes where zooplankton are positioned close to the nearshore littoral zone during the day and migrate to the open pelagic waters during the night. The study of zooplankton DHM could help elucidate predator-prey relationships in lakes because zooplankton is a food source for young-of-year fishes and benthic invertebrates. A better understanding of zooplankton DHM and its effects on other communities, especially young-of -the-year fishes would greatly inform management strategies in both the littoral and pelagic zones of Lake Erie and other lakes.

2. The aim of this study was to establish if DHM of crustacean zooplankton occurs in the western basin of Lake Erie, focusing specifically on how predation (invertebrate and fish) affected zooplankton DHM. A 24-hour period (diel) study was conducted on 6 dates during the summer of 2005 with samples taken at midnight, before sunrise, midday, and before sunset at three sites: 2 nearshore and 1 offshore site. I examined both volumetric (#/L) and areal (#/m^2) densities of zooplankton at each site to determine if zooplankton undergoes DHM. I hypothesized that there would be higher density of crustacean zooplankton in the nearshore sites than the offshore site during the daytime because of high fish predation pressure in the offshore. Contrastingly, I hypothesized there would be a higher density of crustacean zooplankton in the offshore during the nighttime due to reduced predation pressure. At the three sites, invertebrates and fishes were collected at each site to determine the effect of predation on DHM of zooplankton.

3. Zooplankton samples (N=78) were collected using a metered zooplankton net and preserved using a 4% sugar formaldehyde solution and then enumerated under a dissecting microscope with densities calculated using dilution techniques and flow meter data. I determined the densities of three taxa: cladocerans, cyclopoid copepods, and calanoid copepods, and the total of all these taxa combined. Also, I qualitatively examined the number of fishes and calculated zooplanktivorous invertebrate abundance at each site.

4. Zooplankton significantly differed by taxon ($p<0.001$) for volumetric and areal densities, and differed significantly by site ($p<0.001$) and taxon by site ($p=0.001$) for areal densities only. From the two-way ANOVA, there was only significance in cladocerans by site across all times ($p=0.004$) for the volumetric density, but for the areal density there was significance in all the individual taxa (calanoid copepods, cyclopoid copepods, and cladocerans) and total crustacean zooplankton by site ($p<0.001$). Also for the volumetric densities there was a significant difference for calanoid copepods by the interaction of time and site ($p=0.041$). At the offshore site the density of zooplankton decreased to its minimum at midday or pre-sunset and increased towards midnight. At the two nearshore sites the cyclopoid and calanoid copepod densities slightly increased at midday or pre-sunset and decreased afterwards. Biotic factors, such as zooplanktivorous fishes that were found at the nearshore sites and abiotic factors, such as turbulence, were likely responsible for the zooplankton DHM pattern.

INTRODUCTION

The zooplankton is a collection of heterotrophic microorganisms whose position in the water column is greatly affected by water movements. However, the zooplankton is not totally at the mercy of the currents and is known to migrate vertically and horizontally. Diel horizontal migration (DHM) has been observed in zooplankton in shallow lakes where zooplankters are positioned near the littoral zone during the day and migrate to the open pelagic waters during the day (Wicklum 1999, Masson *et al*. 2001, Burks *et al*. 2002, and Romare and Hansson 2003).

Zooplankters generally avoid the littoral zone or nearshore because macrophytes produce chemicals that inhibit zooplankton growth and reproduction (Burks *et al*. 2000, 2001a,b). Burks *et al.* (2000) found that the zooplankter *Daphnia,* living among the aquatic macrophyte *Elodea*, matured later and produced fewer eggs. Macrophytes secrete chemicals as an allelopathic mechanism to impede the growth of phytoplankters that compete for the same resources of light and nutrients. Several studies verified that the density of phytoplankton decreases around macrophytes (Gross 2003, Lüring *et al*. 2006, Mulderij *et al.* 2006) through direct contact or indirectly by being located in the surrounding water where the chemicals are dispersed. Phytoplankton is the main food source for zooplankton and as a result zooplankton is limited by their food source if they stay in the macrophytes. Although studies have found that to increase their chance of survival zooplankters would ignore the costs associated with lower growth and reproduction and hide in the macrophytes when predators were present (Burks *et al.* 2001a, Okun and Mehner 2005). Studies confirm that predation rate on zooplankton is lower within the macrophytes than in open water and this provides a rationale for DHM (Burks 2000, 2001ab, Okun 2005, Van de Meutter *et al.* 2004, 2005). Burks *et al*. (2001a) found that zooplankton preferred to hide in artificial

macrophytes rather than in true macrophytes, but when fish predators or kairomones were present the zooplankton would hide equally in either artificial or real macrophytes. This study shows that zooplankters sense the macrophytes' chemicals and generally stay away from them, but when zooplankters are endangered by predation they instinctively hide in the macrophytes (Burks *et al*. 2001a). Thus, zooplankton use DHM as a "predator avoidance" mechanism and hide in the macrophytes at a cost to growth and reproduction in order to avoid being eaten and increase their chance of survival.

A number of factors may initiate zooplankton DHM. One possibility, known as the "active movement theory" suggests that zooplankton are sensitive to light and exhibit DHM because they would prefer to move out into the illuminated waters rather than stay in the shadows of macrophytes at night. Wicklum (1999) performed a mountain lake study to determine if DHM was caused by the "active movement theory" or fish predation by taking samples of fishless lakes and fish lakes. Without any predators, Wicklum hypothesized that the DHM of zooplankton would be influenced by light. In both types of lakes, Wicklum sampled at the shore, the deepest part of the lake or midlake, and the outlet of the lake. Wicklum concluded that fish predation was the cause for DHM, because during the day 7.9% of zooplankton would be near the shore in the fish lakes, while in the fishless lakes 61.9% of zooplankton would be near the shore. Wicklum suggested that fish predation caused the zooplankton to behave in a reverse DHM (movement away from the shore during the day), because most of the fishes lived in shallow water. Other factors that could cause DHM include light, temperature, pH, and food abundance, but studies have found that the main cause for DHM are predators and their chemical cues called kairomones (Burks *et al*. 2002, Wicklum 1999, Romare and Hansson 2003).

Fishes secrete kairomones that act as chemical messages to other animal species. The composition of kairimones is still unknown, but most likely they are water soluble. Zooplankton can directly detect these kairomones and are affected by them (Von Elert and Pohnert 2000). Weber (2003) found that fish kairomones lead to decrease in age and size of reproduction in *Daphnia*. Furthermore, he found that kairomones produced by different species of fish could differentially alter life history characteristics of *Daphnia*. He found that in the presence of the kairomone of the fish *Perca* the *Daphnia* reproduced at a lower rate than in the presence of kairomones produced by another fish (*Gasterosteus*). Other studies have been done on the absence and presence of predators and the kairomones of invertebrate (Burks *et al.* 2001b, Van de Meutter *et al.* 2004, 2005) and vertebrate predators (mainly fishes) (Burks *et al.* 2001ab, Okun and Mehner 2005). These studies found that zooplankton react equally to the presence of either predators or their kairomones for both vertebrate and invertebrate predators. These studies are consistent with Weber (2003) in which zooplankters react differently to different predators and their kairomones and more so to pelagic predators (Van de Meutter *et al*. 2005, Burks 2001b, Okun and Mehner 2005). Van de Meuuter *et al.* (2005) observed in a lab experiment that zooplankters would remain in the macrophytes in the presence of pelagic predators. Thus, zooplankton can sense the presence and type of predator due to the kairomone production of the predator. It is unclear if zooplankters are more sensitive to the presence of invertebrates or vertebrates, because many studies have been conducted with only two predators of similar taxa (invertebrates vs. invertebrates or fish vs. fish); hence more studies can be done using multiple types of predators (i.e., fish vs. invertebrates).

Diel variation in the horizontal position of zooplankton has been observed in Lake Erie (Kane *et al.* 2005, Stockwell *et al*. 2002). Kane *et al*. (2005) conducted a 24-hour study

to determine if zooplankton underwent DHM. Their results reflected other studies in shallow lakes in which zooplankton migrate into the littoral zone during the day and move into the open pelagic water during the night (Burks *et al.* 2002, Wicklum 1999, Masson *et al.* 2001, Romare and Hansson 2003). Studies have shown that zooplankton would hide during the day from predation in macrophytes in the littoral zone and then at night, when zooplankton are less seen by vertebrate predators (fish), move into the open water to forage for food (Burks *et al*. 2001(b), Romare and Hansson 2003, Lewin *et al*. 2004). However, there are predators in the littoral zone as well (Okun and Mehner, 2005, Van de Meutter *et al*. 2005), especially invertebrates (Burks *et al.* 2001b, Van de Meutter *et al.* 2004)

This study is a continuation of Kane *et al*.'s (2005) study on the distribution of zooplankton in the western basin Lake Erie. I sought to determine if there was a trend in the horizontal distribution of zooplankton and whether that was constant with DHM of zooplankton. I conducted a field study and collected zooplankton that was naturally abundant at three sites: two nearshore and one offshore site. Based on the available literature on zooplankton DHM, I hypothesized that there would be more crustacean zooplankton in the nearshore than the offshore during the daytime (Figure 1), due to high predation pressure in the offshore during the daytime. Contrastingly, I hypothesized there would be more crustacean zooplankton in the offshore during the nighttime (Figure 1), due to reduced predation pressure and greater phytoplankton resources. For predation pressure, I examined the presence of zooplanktivorous fish and invertebrates at each site.

MATERIALS AND METHODS

Study area:

During 20 June to 10 August 2005 this study was conducted in three different habitats in Lake Erie (Figure 2): Alligator Bar, a nearshore site (< 2m from shore); a slightly Offshore site (>10 m from shore), between Peach Point, South Bass Island and Gibraltar Island; and Terwilliger's Pond, a pond-like habitat that is connected to Lake Erie. In my study the offshore differed from Kane *et al.*'s (2005) Offshore site in that is was further offshore (>100 m from shore), was deeper (6-8 m), and contained no macrophytes.

At each site, I looked for four factors that could influence DHM (Table 1). I looked for macrophytes where the zooplankton could hide in during the day, presence of zooplanktivorous invertebrates, presence of zooplanktivorous fish (which are the main vertebrate predators for zooplankton), and turbulence in the water.

Alligator Bar has all four of these factors present. There are macrophytes including *Vallisneria americana* (tape grass) and *Ceratophyllum demersum* (coon tail). The site consists of a mound of cobble and is connected to Gibraltar Island with a water depth less than 3 meters. Alligator Bar is a turbulent area where water is consistently moving to create an unstable environment for organisms to live.

Terwilliger's Pond is a small (about 100 m wide by 50 m long) shallow pond (less than 3 meters deep) that is on South Bass Island. A channel is connected to Lake Erie, allowing flow between the two bodies of water. The substrate of the pond is silty and muddy and within the water there are several macrophytes such as *Nymphaea odorata var. tuberosa* (white water lily). However, my study was conducted outside the channel in 1.5-2 meters of water where macrophytes such as *V. americanana, Potamogeton richardsonii* (Richardson's pondweed), *Myriophyllum spicatum* (Eurasian water milfoil) and *Cladophora* (benthic algae)

are abundant. Like Alligator Bar, Terwilliger's pond has all the factors except its water is calmer making an ideal refuge for organisms to hide from predators.

The Offshore site (near Peach Point) is approximately 6.5-7 meters deep. Like the other sites it has both zooplanktivorous invertebrates and fishes. The substrate is silty and sandy and there are no aquatic macrophytes present.

Based on these characteristics, I hypothesized that the density of zooplankton would differ at each of the three sites during a 24-hour period (Figure 1). I believed that Alligator Bar and Terwilliger's Pond would have the highest densities at midday when the sun is brightest and zooplankters would be using the macrophytes as refugia from visual predators. However, at night the zooplankton would be less likely seen by predators and move out to open waters to forage for food. By midnight, the density of zooplankton would be the greatest at the Offshore site and then gradually decrease by morning as zooplankton return to the macrophytes in the nearshore. I also hypothesized that overall the density of zooplankton in Terwilliger's Pond would be higher than Alligator Bar since there is less water movement and the zooplankton would have a better refuge since there is less an effect of turbulence compared to Alligator Bar.

Zooplankton collection:

Samples were collected with a zooplankton net (0.5 m diameter, 64 μm mesh). A General Oceanics 2030 model flow meter connected to the zooplankton net was used to calculate how far the net traveled and used in zooplankton density calculations (see below). All three sites were sampled using duplicate (up and down) vertical tows to <1 m of the bottom. The zooplankton was preserved in jars of 4 parts of water and 1 part sugar formaldehyde solution: 1 L formaldehyde: 1 L distilled water: 400 grams of sugar (Haney

and Hall 1973). The samples were labeled with information including site, date, time, and flowmeter readings.

Zooplanktivorous invertebrates and fishes:

The invertebrates were collected along with the zooplankton samples using the zooplankton net. The invertebrates were enumerated and used to calculate their density. The fishes were caught by Dr. David Jude (University of Michigan) and Richard Londraville (University of Akron) from June-August 2005. They collected the fishes by seine at Alligator Bar and Terwilliger's Pond and at the Offshore the experimental gillnet was used and set overnight. At each site, the species of fish were recorded. Only time was recorded at Alligator Bar. No data were recorded regarding the period of the day that fishes were found at Offshore and Terwilliger's Pond.

Zooplankton enumeration:

Zooplankton samples were diluted with distilled water to a known volume. A subsample of 10 ml was taken and enumerated using a dissecting microscope. A minimum of 100 individuals of the most abundant taxon was enumerated. If there were fewer than 100 individuals of the most abundant taxon then the entire sample was enumerated. The cladocerans were identified to genus (i.e., *Daphnia*, *Bosmina*, *Diaphanosoma*, and *Leptodora*). Copepods, including their nauplii, were identified to suborder (Calanoida and Cyclopoida). Invertebrate predators such as water mites (Hydracarina*)* and phantom midges (*Chaoborus*) were enumerated and analyzed. Dreissenid veligers, rotifers, and hapacticoid copepods were enumerated but not included in subsequent analyses.

The densities of zooplankton were calculated both using areal (#/L) and volumetric (#/m^2) measurements. The volumetric densities of zooplankton per liter were determined using the number of individuals of each taxon, the meter readings, and dilution subsample volumes. The areal density was determined by multiplying #/L by 1000 to obtain #/m^3 and then by multiplying this volume by the depth of the entire water column. Both the volumetric and areal densities are shown in the following formulae:

Volumetric Density (#/L) =

$$\frac{\text{(\# Individuals in Subsample) (Dilution Volume/ Subsample Volume)}}{\text{(Net Constant = 5.2765 Liters/Revolution) (Revolutions of Flowmeter)}}$$

Areal Density (#/m^2) = (#/L) (1000) (Depth (m))

Statistics:

A Multiple Analysis of Variance (MANOVA) was used to detect differences in mean densities (volumetric and areal) by taxon (Cladocera, Cyclopoida, and Calanoida), time, site, and interactions among taxon, time, and site. Also two-way Analysis of Variance (ANOVA) tests were used to look for density differences among times and sites by taxon and interactions between time and site. An alpha value of 0.05 was used to judge for significance for all of these analyses.

RESULTS

Species composition of zooplankton:

A total of 30,146 zooplankters (Table 2) were enumerated for 6 days of samples (n=78). Cyclopoid copepods were the most abundant taxon with about 20,000 individuals enumerated, with 72% of them being copepodids. The cladocerans and calanoid copepods were in the range of 4,000-5,000 individuals enumerated. 32% of the calanoid copepods were copepodids and 20% of the cladocerans enumerated were *Daphnia*.

Diel pattern of zooplankton volumetric and areal densities:

The diel pattern of the total crustacean zooplankton volumetric (Figure 3d) and areal density (Figure 3h) differed from what I expected (Figure 1). For example, in the offshore sites the minimum for areal and volumetric densities of zooplankton occurred at pre-sunset instead of midnight. The volumetric and areal density diel patterns were similar, but the areal density (Figure 3h) showed a wider range in the number of zooplankton than the volumetric density (Figure 3d) in the offshore. The diel pattern was again similar for the three individual taxa at the offshore in which the areal density (Figures 3e, 3f, and 3g) is shown at a wider range than the density (Figures 3a, 3b, and 3c). Further, zooplankton areal densities in the offshore were consistently greater in the offshore than in either of the nearshore sites (Figures 3 e, 3f, 3g, and 3h).

The diel pattern of the total crustacean zooplankton was similar between the two nearshore sites. Alligator Bar and Terwilliger's Pond were similar to each other for the volumetric (Figure 3d) and areal densities (Figure 3h) of zooplankton. The maximum number of zooplankton at Alligator Bar occurred at midday and decreased afterwards at pre-sunset, but then increased again in volumetric (Figure 3d) and areal (Figure 3h) density. The

volumetric and areal densities of zooplankton at Terwilliger's Pond slightly increased from pre-dawn and continued to increase throughout the day and into the night (Figures 3d and 3h). Looking at the taxa at the two nearshore sites, the cyclopoid copepod (Figures 3b and 3f) diel pattern was the only taxon consistent with the volumetric and areal density diel patterns of the total crustacean zooplankton. The calanoid copepod density (Figures 3a and 3e) increased from pre-dawn to its maximum at pre-sunset instead at midday and decreased through the night. The cladoceran densities (Figures 3b and 3f) were different from the two copepods, where maximum densities were at predawn and decreased through pre-sunset and afterwards increased through midnight.

For the areal densities of all the individual taxa and total crustacean zooplankton (Figures 3e, 3f, 3g, and 3h), the standard error of the Offshore site and nearshore sites did not overlap, which indicates a significant difference between the nearshore sites and the Offshore site. The offshore areal density was higher than the nearshore and varied more; while the nearshore sites' areal densities changed little over time. Furthermore the standard errors were higher in the offshore than the two nearshore site for the areal density. The areal density of the two nearshore site overlapped so there was no significant difference between the two nearshore sites. However, areal densities were typically slightly great at Alligator Bar than at Terwilliger's Pond.

For the volumetric densities of all the individual taxa and total crustacean zooplankton (Figures 3a, 3b, 3c, and 3d), the standard error of all three sites overlapped each other which indicates no significant difference. The volumetric densities of the nearshore sites have a wider range in the number of zooplankton than the areal density graphs (3e, 3f, 3g, and 3h). Similar to the areal densities, the volumetric densities at Alligator Bar were slightly greater than at Terwilliger's Pond.

Seasonal diel pattern:

The pattern of the distribution of taxa and zooplankton varied each day throughout the summer (Figures 4, 5, 6, and 7) in volumetric density and areal density. Towards the end of July to early August the densities were more variable over a 24-hour period. Both the volumetric density and areal density (Figures 4, 5, and 7) had similar diel patterns, except the areal density patterns were vertically stretched. For example, the cyclopoid copepod areal density at Alligator Bar on 29 June (Figure 5d) is relatively higher at midnight than the volumetric density at that exact time (Figure 5a). This pattern is again similar at Terwilliger's Pond on 22 June, 27 July and 3 August where the areal densities (Figure 5f) are similar in pattern to the volumetric density (Figure 5c), but exaggerated vertically. Overall, there were no clear patterns except that during some days there were "V" shaped or "∩" (upside down letter U) shaped diel distributions with the V or ∩ end pointing at midday or pre-sunset. In all the taxa and total crustacean in the nearshore sites the highest zooplankton abundance occurred at midday or pre-sunset and decreased afterwards (Figures 4, 5, 6, and 7). The opposite pattern occurred at the Offshore site in which the lowest densities occurred at midday or pre-sunset and either increased or decreased afterwards. The diel distributions of all three taxa were roughly similar to one another. For example, in the offshore site there would be similar V's or ∩'s shapes when comparing the same taxon for volumetric (Figures 4b, 5b, and 6b) and areal (Figures 4e, 5e, and 6e) densities.

Statistical outcome:

For the MANOVA analyses (Table 3), there was a significant difference in zooplankton volumetric densities by taxon ($p<0.001$) across all times and sites. For areal

densities there was a significant difference in zooplankton densities by taxon ($p<0.001$), site ($p<0.001$), and the interaction between taxon and site ($p<0.001$). From the two-way ANOVA (Table 4), the only significant difference for volumetric densities was in cladocerans by site across all times ($p=0.004$). For the two-way ANOVA for the areal densities there was significance in all the groups (calanoid copepods, cyclopoid copepods, cladocerans, and total crustacean zooplankton) by site. There was also a significant interaction between time and site ($p=0.041$) for calanoid copepod areal densities.

Invertebrates:

Four types of zooplanktivorous invertebrates were found: water mites (hydracarina), phantom midges (*Chaoborus*), platyhelminthes (flatworms), and hydras. 308 zooplanktivorous invertebrates were enumerated and 250 of these were water mites (Table 2). Less than 30 individuals each were phantom midges, flatworms, or hydras (Table 2).

The overall density of zooplanktivorous invertebrates at all three sites was less than 1/L (volumetric density) (Figure 8a) and less than $1000/m^2$ (areal density) (Figure 8b) There were more invertebrates at the nearshore sites (>0.5/L, $>500/m^2$) compared to the Offshore site (<0.1/L, $< 200/m^2$). Alligator Bar had the most invertebrates (>0.8/L, $>800\ m^2$) while the Offshore site had the least (<0.1/L, $< 200/m^2$). The most abundant invertebrates at all the sites were water mites and second most abundant were the hydras and flatworms, while the phantom midges were the least abundant taxon (Table 2, Figures 8a and 8b).

Fishes:

A total of 25 different species of fish were caught at all three sites combined. The fish data illustrates that zooplanktivorous fish species were abundant at Alligator Bar and

Terwilliger's Pond, but not at Offshore site (Table 6). Alligator Bar had the most zooplantivorous fish species where out of 19 species of fish there were 5 zooplanktivores and 3 omnivores and most of these fishes were found at dusk and night. The zooplanktivores included the brook silverside (*Labidesthes sicculus*), emerald shiner (*Notropis atherinoides*), juvenile smallmouth bass (*Micropterus dolomieu*), and white perch (*Morone americana*). The Offshore site had the least with only one zooplanktivore (white perch) and 3 omnivores out of 7 species found. At Terwilliger's Pond, 3 fish species were zooplanktivores and two were omnivores out of 10 species.

DISCUSSION

My results show that there is a difference in densities among taxa in both volumetric and areal density. For the areal density there are changes in the individual taxa at each site and time, but that does not conclusively demonstrate that zooplankton performed DHM. However looking at the mean density of six days at each site and time period there is evidence for DHM (Figure 3d), but not as I hypothesized (Figure 1). At the Offshore site, the zooplankton densities decreased throughout the day from pre-dawn to pre-sunset and then increased at midnight. This pattern may be due to high predation at pre-sunset because the fishes could be migrating into the nearshore where there would be enough light for these visual predators to see and capture zooplankters. Young of the year (YOY) fishes are known to perform reverse DHM (move into the nearshore during night) in order to hide from piscivores during the evening (White 1997, Perrow *et al*. 1999, Kornijow *et al*. 2005, Okun 2005). A study done in mid-summer on a shallow lake in Sweden found that young-of-the year (YOY) fishes were less active at night and hid in the littoral zone away from the piscivores while larger *Daphnia* moved into the open water (Romare and Hansson 2003). With regards to my study, perhaps sunset is the time when the YOY fishes migrate from open water to the nearshore. Zooplankton may be hiding in the nearshore, and as these fish migrate to the nearshore zooplankton may move into offshore areas. Another possibility is that zooplankters migrate further offshore at pre-sunset. They could be further offshore where there is more food and deeper water in which to hide from the YOY fishes. Implications for future studies include more extensive sampling of nearshore sites and offshore sites and determining zooplankton food resource abundance by quantifying phytoplankton density at each site.

There is a significant difference in zooplankton areal densities (Figures 3 e, 3f, 3g, and 3h) between the offshore and nearshore sites. In the offshore, the zooplankton density decreases during the day while in the nearshore zooplankton density remains relatively constant. The zooplankton could be moving to further offshore sites that lead to a density change. However, looking at the volumetric densities (Figures 3a, 3b, 3c, and 3d), even though the standard error bars overlap during some time periods, there are other times when there may be real differences in zooplankton density between the two nearshore sites. In fact, volumetric densities are consistently greater at Alligator Bar, and there are a number of occasions where the standard errors do not overlap (Figures 3a, 3b, 3c, and 3d). The areal density could show less difference between the nearshore sites because the depth of each site was taken into account in the areal calculations and these sites are of similar depth.

A future study could be done to sample beyond the Offshore site and extend the sampling period past midnight to see if zooplankton density increases more as night progresses. More studies could be done to see if DHM is different among taxa during different seasons, especially during the spring phytoplankton peak. According to Lampert *et al.* (1986), the mid-summer decline in zooplankton abundances is part of a phenomenon known as the clear water phase (CWP) that is observed in meso- and eutrophic lakes. The CWP is a 'distinct' period where after an early bloom of algae in the spring the water is clear which increase light penetration in the water. This increased water transparency is likely caused by zooplankton overgrazing the edible algae (Lampert *et al*. 1986, Wu and Culver 1991, Tonno *et al.* 2003). During the CWP, zooplankton populations undergo a mid-summer decline because there are less edible algae, but eventually recover and increase in abundance as more food becomes available. When I began my study in late June, I found that zooplankton was less abundant compared to early August (Table 5, Figure 7). Furthermore,

as the summer progressed, the diel variation in zooplankton abundance was greater (Figure 7). This was a sign that the overall zooplankton crustacean population were recovering from a "mid-summer decline" (Table 5, Figure 7).

Several studies have found that *Daphnia* is the principal grazer of algae and its population is strongly affected by the CWP (Perrow *et al*. 1999, Wu and Culver 1991). Tonno *et al.* (2003) found that during the CWP, even though the overall zooplankton population showed a summer decline, there were more copepods than cladocerans. This is because copepods are better able to eat smaller phytoplankton and thus are better able to survive and reproduce during times of low phytoplankton abundance. This study is consistent with my results in which the most abundant taxon across all times and sites were the cyclopoid copepods and the least abundant were the cladocerans (Table 5, Figure 3b and 3c) Interestingly, the cladoceran density distribution was very much different from the copepods. At Alligator Bar (Figure 3c), the expected DHM pattern occurred where the cladoceran density increased up to the highest peak at midday and dramatically decreased by nightfall. Perhaps the cladocerans rely on macrophytes more than the other taxa and spend most of their time at Alligator Bar because they are larger zooplankters and thus more vulnerable to visual vertebrate predators. Perrow *et al*. (1999) found that vegetation cover was positively associated with *Daphnia* density and believed macrophytes enable the cladoceran to survive during the CWP.

I hypothesized there would be a greater abundance of zooplankton at Terwilliger's Pond than Alligator Bar, but there were fewer zooplankters at the Terwilliger's Pond site compared to the Alligator Bar site. Zooplankters are known to be poor swimmers and smaller zooplankton cannot avoid the shore altogether (Wicklum 1999). However, a study done on *Daphnia* with video computer analysis determined that pelagic cladocerans could

swim up to 24mm/s (Dodson *et al.*1997). Copepods move by hopping once every second, but when threatened can move 30mm/s (Williamson and Reid 2001). The copepod nauplli tend to be more stationary, but can still swim. The fastest recorded swimming burst was 364 body lengths/s (44mm/s) (Williamson and Vaderploeg 1988 cited in Willamson and Reid 2001). Consistent with zooplankton movement, for the cladocerans (Figure 3c) and other taxa on individual days (Figures 4, 5, 6, and 7) there were sharp decrease in densities after midday or midnight.

An alternate possibility to voluntary movement is involuntary movement of zooplankton due to water movements, including turbulent mixing. I believe that turbulence could be an advantage because the water could move macrophyte chemicals away from shore so as to lessen the negative effects of these chemicals on zooplankton growth. The water currents also make it difficult for fish to catch the zooplankton. Turbulence in water could be advantageous for zooplankton, but not much is known about the efficiency by which zooplankton can swim in turbulent water.

Wicklum (1999) indicated that zooplankton actively avoid lake outlets, but only implied that the environment was constantly changing in a way not suitable for zooplankton. Perhaps, zooplankters were avoiding Terwilliger's Pond because of the different water composition from Lake Erie. Possibly the zooplankton avoided Terwilliger's Pond because they were not able to adapt quickly to the changes in the two bodies of water that intermix from where we sampled. Yet, on 27 July 2005 there was storm and there was an increase in zooplankton abundance at Terwilliger's Pond, which could be evidence that the area was used as refuge or that zooplankters were forced to move into the area by water currents. With more movement in the water and more connection to the offshore, the zooplankton may prefer Alligator Bar over Terwilliger's Pond. The turbulence in the water at Alligator Bar

would also create a turbid environment. With more turbidity, the zooplankton would be less seen and less likely to perform DHM during the day. Thus in future studies, light penetration could be determined in order to determine its effect on DHM. There could be considerably more research performed on water movements that could be done in a lab to quantify the water movement and the how these movements affect zooplankton DHM.

There was a greater density of invertebrates and more fish species at the nearshore sites compared to the offshore site. This reflects other studies that these animals rely on macrophytes as a refuge (Kornijow *et al.* 2005, Okun 2005). At Alligator Bar zooplankton, invertebrates, and fish species were more abundant, which suggests that Alligator Bar is an ideal refuge for many organisms. Romare *et al.* (2003) found that small fishes generally hide at the edge of the vegetative zone during the day and in another study Nurminen and Horppila 2001 found that *Daphnia* had a high density in the outer vegetative zone. The zooplankton and fishes may prefer Alligator Bar because the site is closer to the open water so the organisms can move in and out of the macrophytes easily to avoid predators, but still can move into open waters for foraging.

The DHM of zooplankton is likely caused more by fish than invertebrates because fishes are active predators and able to swim from the pelagic zone to littoral zone. However, it is still unclear if fishes do cause zooplankton DHM because I only examined the number of species that were present in the three sites and when they were caught was only recorded at Alligator Bar. By looking at the vertebrate predators quantitatively and determining how they vary through time, I may be able to better explain the patterns I found in the horizontal distribution of zooplankton in the western basin of Lake Erie.

For future studies, I could also quantify the macrophytes and phytoplankton abundance at each site. I noticed an increase in detritus in the zooplankton samples that

accompanied the senescence of aquatic macrophytes. The impact of the increase of detritus (and increased bacterial food resources for zooplankton) on DHM also deserves attention. I could also look at climate and other seasonal factors and how they may affect DHM. A three-year study done by Romare *et al*. (2005) found that zooplankton abundance and composition varied by season and was affected by climatic factors such as temperature.

Predators also vary through the season, which could influence zooplankton DHM. One concept, known as the match and mismatch hypothesis deals with fish that have a fixed spawning period. This may be problem because the cohort of larval fish could miss the cycle of phytoplankton and zooplankton that varies throughout the year if they hatch at the wrong time, especially if they miss the phytoplankton and zooplankton peak in abundance that occurs in the spring (Cushing 1974, 1990). If a mismatch occurs, it would affect all trophic levels, especially fish and zooplankton. During the CWP when the food sources of both fish and zooplankton are of low abundance in the offshore, fish and zooplankton could migrate and spend more time hiding in the macrophytes since they are weak and susceptible for predation. The zooplankton could also perform reverse DHM where they would be in the open water to avoid the YOY fish that are hiding in the macrophytes (Burks *et al.* 2000, Nurminen and Horpilla 2001, Romare *et al.* 2003b). If a match occurs, perhaps the zooplankton would perform normal DHM or none at all if the zooplankton population was high enough or the chances of being eaten in the open water was less than being eaten while hiding in the macrophytes. Therefore conducting a long term study on DHM of fishes and zooplankton could be considered in order to understand predator-prey interactions over a longer period of time and look at how the food resource phytoplankton change overtime especially when the macrophytes begin to die in the late summer..

A potential flaw in this study is that I assumed that zooplankton could migrate from site to site within a 24-hour period. There is no extensive research on how far zooplankters can travel, but it has been observed that they could move at least 30 m horizontally and 100 m vertically in a day (Burks *et al.* 2000). Burks *et al.* (2000) state that there is no technology to accurately determine if zooplankton undergo DHM in a natural setting. Many of the field studies on DHM are based on inferring that density differences between nearshore stations and offshore stations are indications of DHM. Further, most of these studies use a zooplankton net or a tube to collect a whole water sample with a filtering device (White 1997, Wicklum 1999, Kane *et al*. 2005, Masson *et al.* 2001, Kornijow *et al* 2005). However, Burks *et al.* (2000) believe that flaws with such studies lie in the fact that zooplankton could be in or near the sediments.

A number of innovative techniques have been developed to circumvent some of the problems found in previous DHM studies. Wojital *et al*. (2003) designed an innovative way to observe DHM of zooplankton by placing bottle traps with filter paper in the water. At each site they set two bottles against each other, one pointing towards the vegetated nearshore zone and another in the opposite direction towards the open water. The zooplankton would swim into the traps and the researchers would collect the samples at different times of the day. This technique is effective because it causes fewer disturbances in the environment and would not disrupt the DHM behavior of zooplankter and could be placed near the sediment. Using zooplankton nets and other filtering device could disrupt the zooplankter behavior and they may be avoiding the nets altogether. The problem with using the Wojital *et al.* (2003) method is that it does not differentiate between current movements which could transport a zooplankter passively into the trap from active swimming by a zooplankter. Another problem is that the zooplankter may swim at different directions and

different water depth to avoid the bottles altogether. There are problems using Wojital *et al*. method, but it may provide insight to DHM zooplankton in a more natural setting. Another innovative technique was used in a study done by Stockwell *et al.* (2002) and looked at the horizontal distribution of zooplankton across Lake Erie using an optical plankton counter (OPC) that uses light particles to sample zooplankton biomass. The problem with using this machine is that it could only be used at the spatial scale of kilometers. Using OPC would not allow one to observe DHM between sites as near to one another as my three study sites.

Another suggestion to improve DHM studies is to take some zooplankters from either the offshore or nearshore site and mark them with some form of dye and release them from the depth from which they were taken to minimize the effect of current on zooplankton movement. After a period of time, samples can be taken from nearby areas and one can calculate the rate and direction of movement of the dyed individuals once they are recaptured. Another possibility is taking DNA samples to look at the population structure of zooplankton. There are zooplankters that prefer habitats nearer to the bottom and one could determine which populations of zooplankton migrate in the water column and which do not.

Another possibility is that I could make more sites within the current area of study and some outside this range. In addition, I could increase the sampling frequency to hourly collections. The problem with this strategy is that it would take more time to enumerate and analyze results. A suggestion to study the overall migration of zooplankton in a large body of water is to divide a project into four parts. First is to determine the distributions and abundance of benthic invertebrates; second, young-of-the-year and other zooplanktivorous fishes; and third, zooplankton, and fourth macrophyte coverage and phytoplankton. I could then combine these four studies to determine the interactions among these communities.

Diel vertical migration (DVM) could also be integrated into the study. A study by Masson *et al.* (2001) on the mountain lakes in France found that zooplankton undergo both DVM and DHM simultaneously another study have found that DVM and DHM are influenced by abiotic factors such as temperature and oxygen (Pinel-Alloul *et al.* 2004). In my experiment I excluded studying DVM since the zooplankton net went close to the bottom at each site, but it would be interesting to determine if zooplankton exhibit both behaviors.

Studying DHM of zooplankton is important to determine predator-prey relationships in lakes. Zooplankton DHM affects other communities, such as the benthic invertebrate and fish communities. A better understanding of where young-of -the-year fishes migrate to follow zooplankton food sources would greatly inform fish management strategies in both the littoral and pelagic zones of Lake Erie and other lakes.

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Table 1- Factors hypothesized to affect Diel Horizontal Migration (DHM) of crustacean zooplankton at three sites in the western basin of Lake Erie (2005).

	Macrophytes	Invertebrates	Fish	Turbulence	Depth
Alligator Bar	Yes	Yes	Yes	Yes	~2m
Terwilliger's Pond	Yes	Yes	Yes	No	~1m
Offshore	No	Yes	Yes	Yes	~7m

Table 2- Number of individuals counted for 6 days of samples (n=78).

Taxon	# of individuals	Taxon	# of individuals
Calanoid nauplii	1357	**Platyhelminthes**	24
Calanoid copepodids	2856	**Hydracarina**	8
Cyclopoid nauplii	15092	***Chaoborus***	250
Cyclopoid copepodids	5690	***Hydra***	26
Daphnia	1080		
Other cladocerans	4071		
Total Crustacean Zooplankton	30146	**Total invertebrates**	308

Table 3 - MANOVA results for volumetric (left) and areal (right) density differences by taxon, time, site and interactions among taxon, time, and site for crustacean zooplankton Diel Horizontal Migration (DHM) study in the western basin of Lake Erie (2005).

	Volumetric (#/L)				Areal (#/m^2)			
	d.f.	F-value	Wilks' λ	P-value	d.f.	F-value	Wilks' λ	P-value
Taxon	2	30.85	0.745	**<0.001**	2	21.18	0.809	**<0.001**
Time	3	0.23	0.996	0.877	3	1.09	0.982	0.356
Site	2	2.91	0.969	0.057	2	27.07	0.769	**<0.001**
Taxon X Time	6	0.29	0.991	0.943	6	0.40	0.987	0.876
Taxon X Site	4	2.19	0.954	0.072	4	4.88	0.902	**0.001**
Time X Site	6	0.57	0.981	0.757	6	1.49	0.953	0.184
Taxon X Time X Site	12	0.36	0.977	0.977	12	0.56	0.964	0.870

Table 4 - Two-Way ANOVA results for volumetric (left) and areal (right) density differences among times and sites by taxon for crustacean zooplankton Diel Horizontal Migration (DHM) study in the western basin of Lake Erie (2005).

Volumetric (#/L)				Areal (#/m^2)			
Taxon	**d.f.**	**F-value**	**P-value**	**Taxon**	**d.f.**	**F-value**	**P-value**
Calanoid Copepods				**Calanoid Copepods**			
Time	3	0.29	0.836	Time	3	0.64	0.592
Site	2	1.33	0.271	Site	2	27.17	**<0.001**
Interaction	6	1.07	0.390	Interaction	6	2.36	**0.041**
Cyclopoid Copepods				**Cyclopoid Copepods**			
Time	3	0.25	0.864	Time	3	0.67	0.572
Site	2	2.30	0.109	Site	2	11.53	**<0.001**
Interaction	6	0.42	0.861	Interaction	6	0.95	0.466
Cladocerans				**Cladocerans**			
Time	3	0.79	0.507	Time	3	0.38	0.765
Site	2	6.19	**0.004**	Site	2	15.29	**<0.001**
Interaction	6	0.14	0.990	Interaction	6	0.26	0.954
Total Crustaceans				**Total Crustaceans**			
Time	3	0.17	0.918	Time	3	0.62	0.607
Site	2	2.22	0.117	Site	2	15.26	**<0.001**
Interaction	6	0.73	0.627	Interaction	6	0.84	0.547

Table 5- Volumetric (#/L) and areal (#/m^2) densities of crustacean zooplankton by date, time period, taxon, and site for crustacean zooplankton Diel Horizontal Migration (DHM) study in the western basin of Lake Erie (2005). Note that Pre-Dawn sampling was conducted on July 28, rather than July 27, due to a storm event.

			Volumetric (#/L)			Areal (#/m^2)		
Date	**Time**	**Taxon**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**
June 22 2005	**Pre-Dawn**	**Calanoid Copepods**	1.40	3.04	3.69	1401.93	21313.47	5533.53
June 22 2005	**Midday**	**Calanoid Copepods**	1.32	1.39	0.92	1987.20	10408.65	1846.60
June 22 2005	**Pre-Sunset**	**Calanoid Copepods**	0.94	1.10	0.99	1412.23	8269.48	1985.44
June 22 2005	**Midnight**	**Calanoid Copepods**	1.57	1.81	3.55	3149.12	14509.04	7098.62
June 22 2005	**Pre-Dawn**	**Cyclopoid Copepods**	3.32	4.14	17.97	3317.89	29011.46	26950.34
June 22 2005	**Midday**	**Cyclopoid Copepods**	5.81	9.18	6.42	8721.58	68831.42	12833.88
June 22 2005	**Pre-Sunset**	**Cyclopoid Copepods**	7.34	8.68	9.02	11015.37	65105.77	18049.48
June 22 2005	**Midnight**	**Cyclopoid Copepods**	11.71	7.34	7.02	23413.02	58707.88	14039.50
June 22 2005	**Pre-Dawn**	**Cladocerans**	1.14	1.38	4.58	1144.91	9635.57	6865.68
June 22 2005	**Midday**	**Cladocerans**	0.63	0.82	0.55	3256.79	6155.655	1107.96
June 22 2005	**Pre-Sunset**	**Cladocerans**	0.21	1.33	0.77	317.751	9975.885	1534.21
June 22 2005	**Midnight**	**Cladocerans**	0.86	2.92	0.28	1711.48	23375.68	552.12
June 22 2005	**Pre-Dawn**	**Total Crustacean Zooplankton**	5.86	8.57	26.23	5864.72	59960.50	39349.55
June 22 2005	**Midday**	**Total Crustacean Zooplankton**	7.76	11.39	7.89	13965.57	85395.73	15788.44
June 22 2005	**Pre-Sunset**	**Total Crustacean Zooplankton**	8.50	11.11	10.78	12745.34	83351.14	21569.13
June 22 2005	**Midnight**	**Total Crustacean Zooplankton**	14.14	12.07	10.85	28273.61	96592.61	21690.24

Table 5- cont'd .

			Volumetric (#/L)			Areal (#/m^2)		
Date	**Time**	**Taxon**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**
June 29 2005	**Pre-Dawn**	**Calanoid Copepods**	1.75	2.61	0.92	2624.12	20898.37	1847.816
June 29 2005	**Midday**	**Calanoid Copepods**	0.46	0.74	0.38	685.32	5913.01	752.5042
June 29 2005	**Pre-Sunset**	**Calanoid Copepods**	0.78	1.60	0.91	1173.85	12786.86	1819.388
June 29 2005	**Midnight**	**Calanoid Copepods**	8.41	0.73	0.73	16829.34	5848.62	1457.843
June 29 2005	**Pre-Dawn**	**Cyclopoid Copepods**	22.67	38.21	19.25	34004.18	305689.90	38496.16
June 29 2005	**Midday**	**Cyclopoid Copepods**	16.30	7.28	3.18	24442.95	58220.41	6354.48
June 29 2005	**Pre-Sunset**	**Cyclopoid Copepods**	3.21	23.62	8.89	4815.18	188989.80	17789.57
June 29 2005	**Midnight**	**Cyclopoid Copepods**	24.22	10.63	13.58	48441.20	85018.89	27152.32
June 29 2005	**Pre-Dawn**	**Cladocerans**	2.70	15.73	1.69	4045.51	125800.00	3387.662
June 29 2005	**Midday**	**Cladocerans**	0.15	2.37	0.15	228.44	18989.86	292.6405
June 29 2005	**Pre-Sunset**	**Cladocerans**	0.14	8.09	1.01	215.61	64701.51	2021.542
June 29 2005	**Midnight**	**Cladocerans**	1.36	7.92	3.83	2729.08	63336.22	7653.675
June 29 2005	**Pre-Dawn**	**Total Crustacean Zooplankton**	27.12	56.55	21.87	40673.81	452388.30	43731.64
June 29 2005	**Midday**	**Total Crustacean Zooplankton**	16.90	10.39	3.70	25356.70	83123.28	7399.624
June 29 2005	**Pre-Sunset**	**Total Crustacean Zooplankton**	4.14	33.31	10.82	6204.64	266478.20	21630.5
June 29 2005	**Midnight**	**Total Crustacean Zooplankton**	34.00	19.28	18.13	67999.62	154203.70	36263.84

Table 5- cont'd.

			Volumetric (#/L)			Areal (#/m^2)		
Date	**Time**	**Taxon**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**
July 20 2005	**Pre-Dawn**	**Calanoid Copepods**	1.33	3.52	0.64	1334.22	24619.59	1288.73
July 20 2005	**Midday**	**Calanoid Copepods**	7.81	2.74	0.56	7809.07	19190.59	840.07
July 20 2005	**Pre-Sunset**	**Calanoid Copepods**	3.05	1.87	3.40	3046.35	13075.19	5097.30
July 20 2005	**Midnight**	**Calanoid Copepods**	4.09	2.39	2.91	4090.84	16715.63	4367.12
July 20 2005	**Pre-Dawn**	**Cyclopoid Copepods**	4.77	9.18	6.56	4770.84	64251.12	13121.65
July 20 2005	**Midday**	**Cyclopoid Copepods**	17.05	1.50	5.79	17052.45	10482.26	8680.77
July 20 2005	**Pre-Sunset**	**Cyclopoid Copepods**	7.12	4.22	8.94	7124.53	29507.53	13408.12
July 20 2005	**Midnight**	**Cyclopoid Copepods**	8.94	8.53	12.4	12072.95	59698.66	18600.69
July 20 2005	**Pre-Dawn**	**Cladocerans**	3.72	0.69	0.41	3719.64	4803.82	820.10
July 20 2005	**Midday**	**Cladocerans**	5.10	0.81	0.37	5099.80	5644.29	560.05
July 20 2005	**Pre-Sunset**	**Cladocerans**	3.69	3.91	0.66	3685.10	27387.23	1108.11
July 20 2005	**Midnight**	**Cladocerans**	2.99	5.71	0.54	3093.07	39292.58	646.98
July 20 2005	**Pre-Dawn**	**Total Crustacean Zooplankton**	9.82	13.38	7.62	9824.69	93674.54	15230.48
July 20 2005	**Midday**	**Total Crustacean Zooplankton**	29.96	5.05	6.72	29961.32	35317.15	10080.89
July 20 2005	**Pre-Sunset**	**Total Crustacean Zooplankton**	13.86	10.00	13.00	13855.99	69969.96	19613.53
July 20 2005	**Midnight**	**Total Crustacean Zooplankton**	16.02	16.62	15.85	19256.86	115706.90	23614.79

Table 5- cont'd.

			Volumteric (#/L)			Areal (#/m^2)		
Date	**Time**	**Taxon**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**
July 28 2005	**Pre-Dawn**	**Calanoid Copepods**	3.19	2.75	4.40	3189.03	19226.62	4403.96
July 27 2005	**Midday**	**Calanoid Copepods**	2.14	2.92	6.80	2141.46	20458.98	10206.98
July 27 2005	**Pre-Sunset**	**Calanoid Copepods**	9.91	2.47	4.97	9906.71	17308.82	7462.33
July 27 2005	**Midnight**	**Calanoid Copepods**	1.72	2.56	2.68	1718.90	17924.34	5369.72
July 28 2005	**Pre-Dawn**	**Cyclopoid Copepods**	13.21	3.64	9.49	13211.70	25475.28	9485.45
July 27 2005	**Midday**	**Cyclopoid Copepods**	6.42	4.49	20.76	6424.39	31434.37	31144.38
July 27 2005	**Pre-Sunset**	**Cyclopoid Copepods**	23.98	2.98	11.02	23977.10	20882.25	16523.74
July 27 2005	**Midnight**	**Cyclopoid Copepods**	7.14	5.56	9.21	7140.04	38914.68	18425.51
July 28 2005	**Pre-Dawn**	**Cladocerans**	1.64	0.84	0.34	1640.07	5864.12	483.95
July 27 2005	**Midday**	**Cladocerans**	0.43	1.13	1.92	428.29	7991.79	3402.33
July 27 2005	**Pre-Sunset**	**Cladocerans**	1.58	0.94	1.85	1722.91	6700.19	3091.54
July 27 2005	**Midnight**	**Cladocerans**	1.06	0.86	1.00	1123.90	6014.09	1895.20
July 28 2005	**Pre-Dawn**	**Total Crustacean Zooplankton**	18.04	7.22	14.23	18040.81	50566.02	14373.37
July 27 2005	**Midday**	**Total Crustacean Zooplankton**	8.99	8.54	29.49	8994.15	59885.14	44753.69
July 27 2005	**Pre-Sunset**	**Total Crustacean Zooplankton**	35.46	6.40	45.48	35606.71	44891.25	27077.61
July 27 2005	**Midnight**	**Total Crustacean Zooplankton**	9.92	8.98	12.90	9982.83	62853.11	25690.43

Table 5- cont'd.

			Volumteric (#/L)			Areal (#/m^2)		
Date	**Time**	**Taxon**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**
Aug 3 2005	**Pre-Dawn**	**Calanoid Copepods**	1.40	3.04	3.69	2842.79	46866.08	1105.53
Aug 3 2005	**Midday**	**Calanoid Copepods**	0.74	1.08	4.55	739.59	7556.81	6819.39
Aug 3 2005	**Pre-Sunset**	**Calanoid Copepods**	16.52	1.30	6.58	16515.28	9069.76	9870.81
Aug 3 2005	**Midnight**	**Calanoid Copepods**	4.94	2.81	6.26	4943.99	19663.80	6264.68
Aug 3 2005	**Pre-Dawn**	**Cyclopoid Copepods**	16.03	20.73	6.05	16033.36	165833.80	9081.15
Aug 3 2005	**Midday**	**Cyclopoid Copepods**	6.47	4.83	29.55	6471.40	33795.74	44326.03
Aug 3 2005	**Pre-Sunset**	**Cyclopoid Copepods**	66.60	2.63	12.90	66602.59	18393.21	19346.79
Aug 3 2005	**Midnight**	**Cyclopoid Copepods**	45.16	14.34	40.90	45155.10	100388.90	40904.64
Aug 3 2005	**Pre-Dawn**	**Cladocerans**	9.21	9.69	0.74	9210.65	77509.29	1263.46
Aug 3 2005	**Midday**	**Cladocerans**	1.02	1.74	0.83	1016.93	12279.82	3099.72
Aug 3 2005	**Pre-Sunset**	**Cladocerans**	5.41	1.40	0.44	5685.59	9767.43	658.05
Aug 3 2005	**Midnight**	**Cladocerans**	12.20	11.74	1.11	12195.17	81316.45	1474.04
Aug 3 2005	**Pre-Dawn**	**Total Crustacean Zooplankton**	28.09	36.28	7.53	28086.80	290209.20	11450.14
Aug 3 2005	**Midday**	**Total Crustacean Zooplankton**	8.23	7.65	34.92	8227.92	53632.37	54245.14
Aug 3 2005	**Pre-Sunset**	**Total Crustacean Zooplankton**	88.53	5.32	19.92	88803.45	37230.40	29875.65
Aug 3 2005	**Midnight**	**Total Crustacean Zooplankton**	62.29	28.89	48.27	62294.26	201369.10	48643.36

Table 5- cont'd.

			Volumteric (#/L)			Areal (#/m^2)		
Date	**Time**	**Taxon**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**	**Alligator Bar**	**Offshore**	**Terwilliger's Pond**
Aug 10 2005	**Pre-Dawn**	**Calanoid Copepods**	0.39	3.83	0.09	392.11	26830.86	136.30
Aug 10 2005	**Midday**	**Calanoid Copepods**	7.20	8.71	0.34	7195.82	60945.31	507.64
Aug 10 2005	**Pre-Sunset**	**Calanoid Copepods**	0.13	1.28	0.81	125.70	8954.80	806.74
Aug 10 2005	**Midnight**	**Calanoid Copepods**	3.75	0.65	0.07	3752.49	4522.92	101.93
Aug 10 2005	**Pre-Dawn**	**Cyclopoid Copepods**	33.13	44.00	8.63	33133.25	307995.90	12948.34
Aug 10 2005	**Midday**	**Cyclopoid Copepods**	131.92	51.35	17.60	131923.40	359421.10	26397.37
Aug 10 2005	**Pre-Sunset**	**Cyclopoid Copepods**	20.74	13.36	10.85	20740.79	93527.91	10846.15
Aug 10 2005	**Midnight**	**Cyclopoid Copepods**	52.53	7.43	2.19	52534.82	52013.57	3287.33
Aug 10 2005	**Pre-Dawn**	**Cladocerans**	5.29	9.66	0.45	5293.48	67636.13	681.49
Aug 10 2005	**Midday**	**Cladocerans**	4.80	22.03	0.90	4797.21	154186.40	1353.71
Aug 10 2005	**Pre-Sunset**	**Cladocerans**	0.75	5.06	0.72	754.21	35421.21	717.10
Aug 10 2005	**Midnight**	**Cladocerans**	3.75	2.54	0.41	3752.49	17768.61	611.60
Aug 10 2005	**Pre-Dawn**	**Total Crustacean Zooplankton**	38.82	57.49	9.18	38818.84	402462.90	13084.64
Aug 10 2005	**Midday**	**Total Crustacean Zooplankton**	143.92	82.08	18.84	143916.40	574552.80	28258.72
Aug 10 2005	**Pre-Sunset**	**Total Crustacean Zooplankton**	21.62	19.70	12.37	21620.70	137903.90	12369.99
Aug 10 2005	**Midnight**	**Total Crustacean Zooplankton**	60.04	10.62	2.67	60039.80	74305.10	4000.86

Table 6- Fish species present at three sites in the western basin of Lake Erie (2005). Data courtesy of David Jude (University of Michigan) (Alligator Bar (fish collected July 29-30 by seine) and Offshore) and Richard Londraville (University of Akron) (Terwilliger's Pond (fish collected during June and July 2005 by seine)). Feeding Guilds: I = Invertivore (including insects), P = Piscivore, **O = Omnivore**, **ZP = Zooplanktivore.** n/a = not applicable.

Site	Species	Scientific Name	Feeding Guild	Most Abundant Time Period
Alligator Bar	Pumpkinseed	*Lepomis gibbosus*	I	Day and Dusk
	Logperch Darter	*Percina caprodes*	I	Dawn and Dusk
	Largemouth Bass	*Micropterus salmoides*	P	Dawn and Dusk
	Brook Silverside	*Labidesthes sicculus*	**ZP**	**Dawn and Dusk**
	Emerald Shiner	*Notropis atherinoides*	**ZP**	**Dusk and Night**
	Yellow Perch	*Perca flavescens*	I	Dusk and Night
	Yellow Bullhead	*Ameiurus natalis*	I	Night and Day
	Bluegill	*Lepomis macrochirus*	I	Dusk
	Smallmouth Bass	*Micropterus dolomieu*	P	Dusk
	Sand Shiner	*Notropis stramineus*	**ZP**	**Night**
	Spottail Shiner	*Notropis hudsonius*	**ZP**	**Night**
	White Perch	*Morone americana*	**ZP**	**Night**
	White Bass	*Morone chrysops*	P	Night
	Rock Bass	*Ambloplites rupestris*	I	Night
	Round Goby	*Neogobius melanostomus*	I	Night
	Freshwater Drum	*Aplodinotus grunniens*	I	Night
	Bluntnose Minnow	*Pimephales notatus*	**O**	**Night**
	Gizzard Shad	*Dorosoma cepedianum*	**O**	**Night**
	Common Carp	*Cyprinus carpio*	**O**	**Night**
Offshore	**White Perch**	*Morone americana*	**ZP**	n/a
	White Bass	*Morone chrysops*	P	n/a
	Common Carp	*Cyprinus carpio*	**O**	n/a
	Gizzard Shad	*Dorosoma cepedianum*	**O**	n/a
	Goldfish	*Carassius auratus*	**O**	n/a
	Brown Bullhead	*Ameiurus nebulosus*	I	n/a
	Freshwater Drum	*Aplodinotes grunniens*	I	n/a
Terwilliger's Pond	**Smallmouth Bass (juveniles)**	*Micropterus dolomieu*	**ZP**	n/a
	Largemouth Bass (juveniles)	*Micropterus salmoides*	ZP	n/a
	Emerald Shiner	*Notropis atherinoides*	ZP	n/a
	Longnose Gar	*Lepisosteus osseus*	P	n/a
	Fathead Minnow	*Pimephales promelas*	**O**	n/a
	Bluntnose Minnow	*Pimephales notatus*	**O**	n/a
	Black Crappie	*Pomoxis nigromaculatus*	I	n/a
	Rock Bass	*Ambloplites rupestris*	I	n/a
	Black Bullhead	*Ameiurus melas*	I	n/a
	Pumpkinseed	*Lepomis gibbosus*	I	n/a
	Bluegill	*Lepomis macrochirus*	I	n/a

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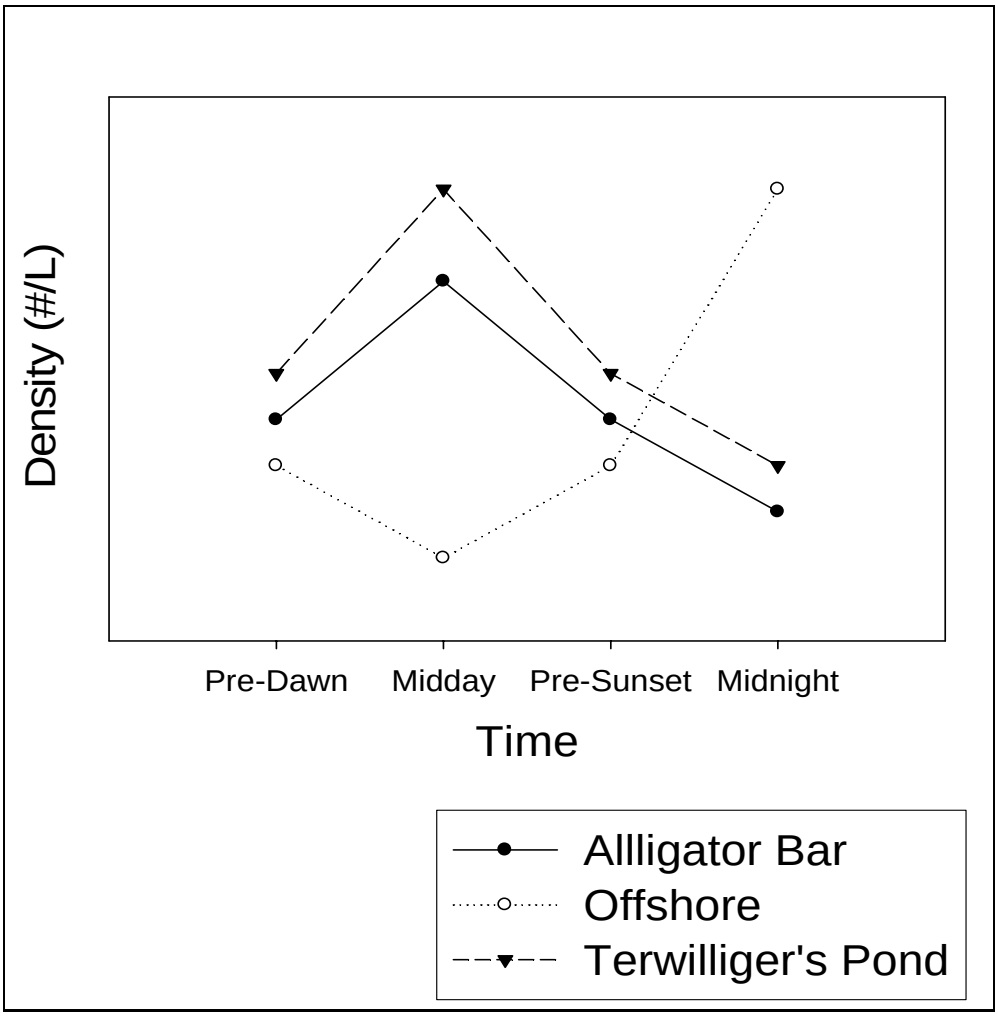

Figure 1- Hypothesized changes of densities of crustacean zooplankton at three sites in the western basin of Lake Erie over a 24-hour period.

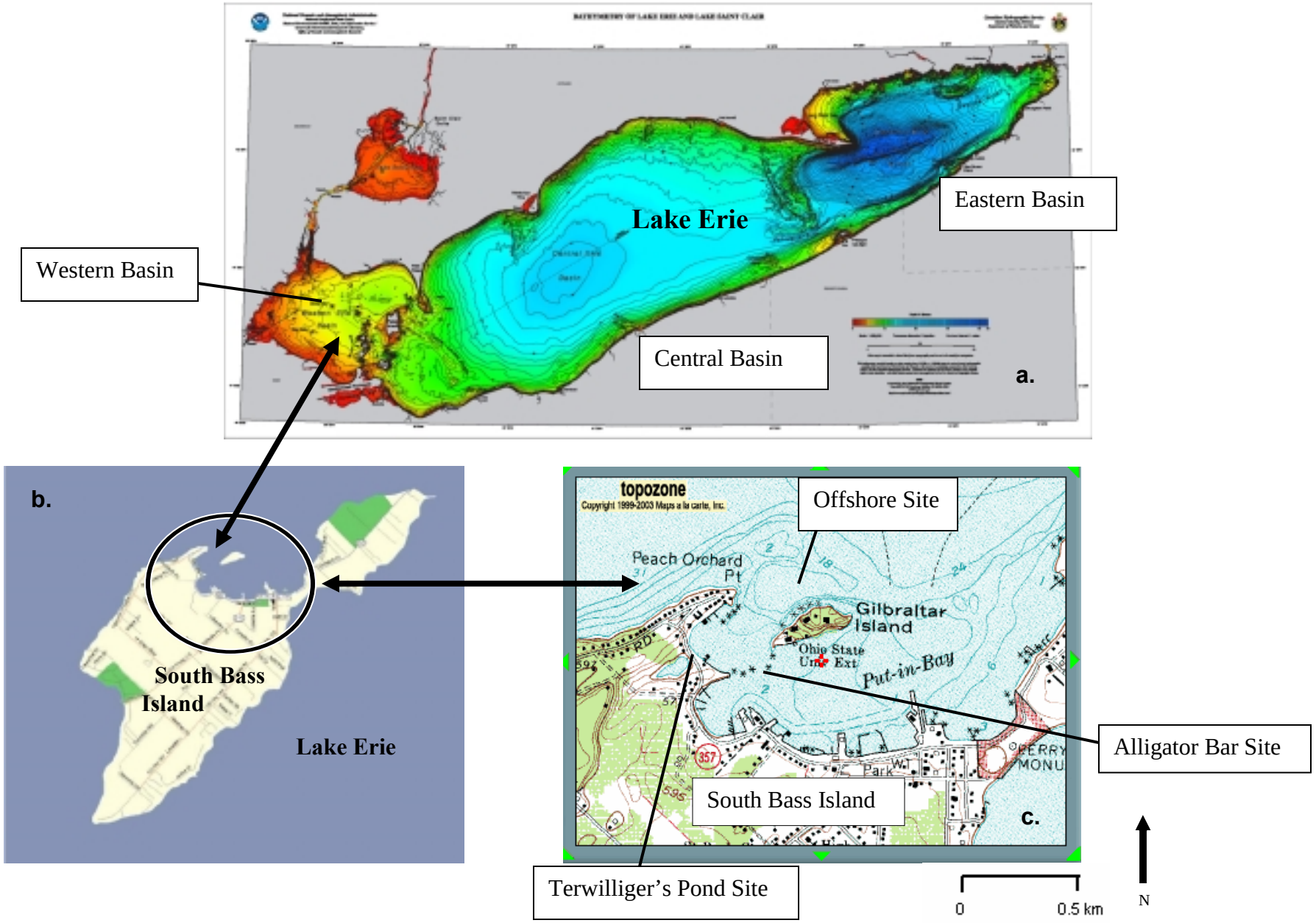

Figure 2- Location of the sampling sites within the western basin of Lake Erie. The uppermost image (a,) shows the three basins of Lake Erie (NOAA 1998): western, central, and eastern basin (from left to right). The image to the lower left (b) is South Bass Island (Put-in-Bay Chamber of Commerce 2006), which is where the three sites are study located. The image to the lower right (c) is a close up view of the three study sites (Topo Map 2006).

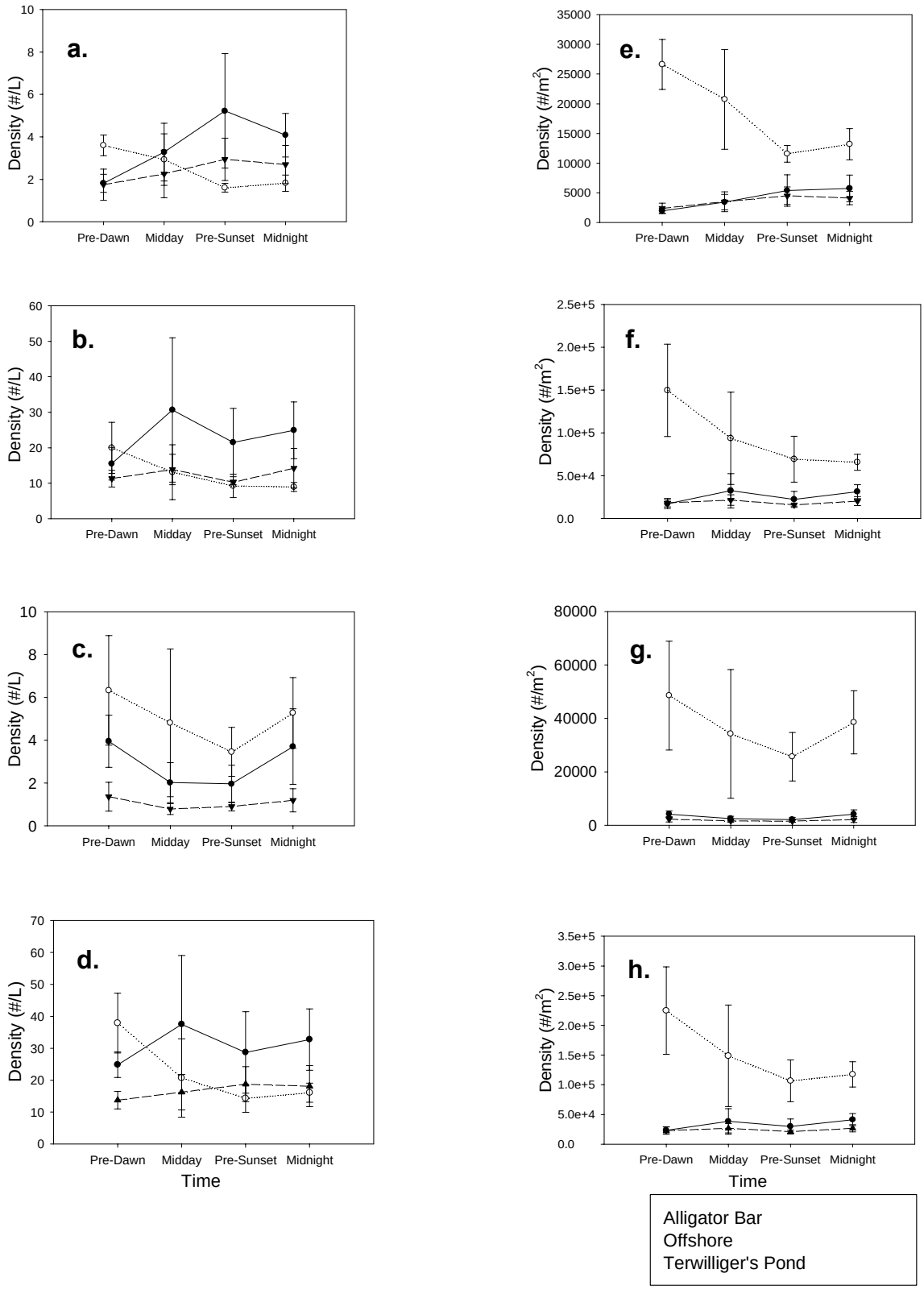

Figure 3- Left: Calanoid copepod (a), cyclopoid copepod (b), cladoceran (c), and total crustacean zooplankton (d) volumetric densities (mean ± standard error); right: calanoid copepod (e), cyclopoid copepod (f), cladoceran (g), and total crustacean zooplankton (h) areal densities (mean ± standard error) at three sites in the western basin of Lake Erie of 6 days during the summer of 2005. Note: the scales are different for each graph panel.

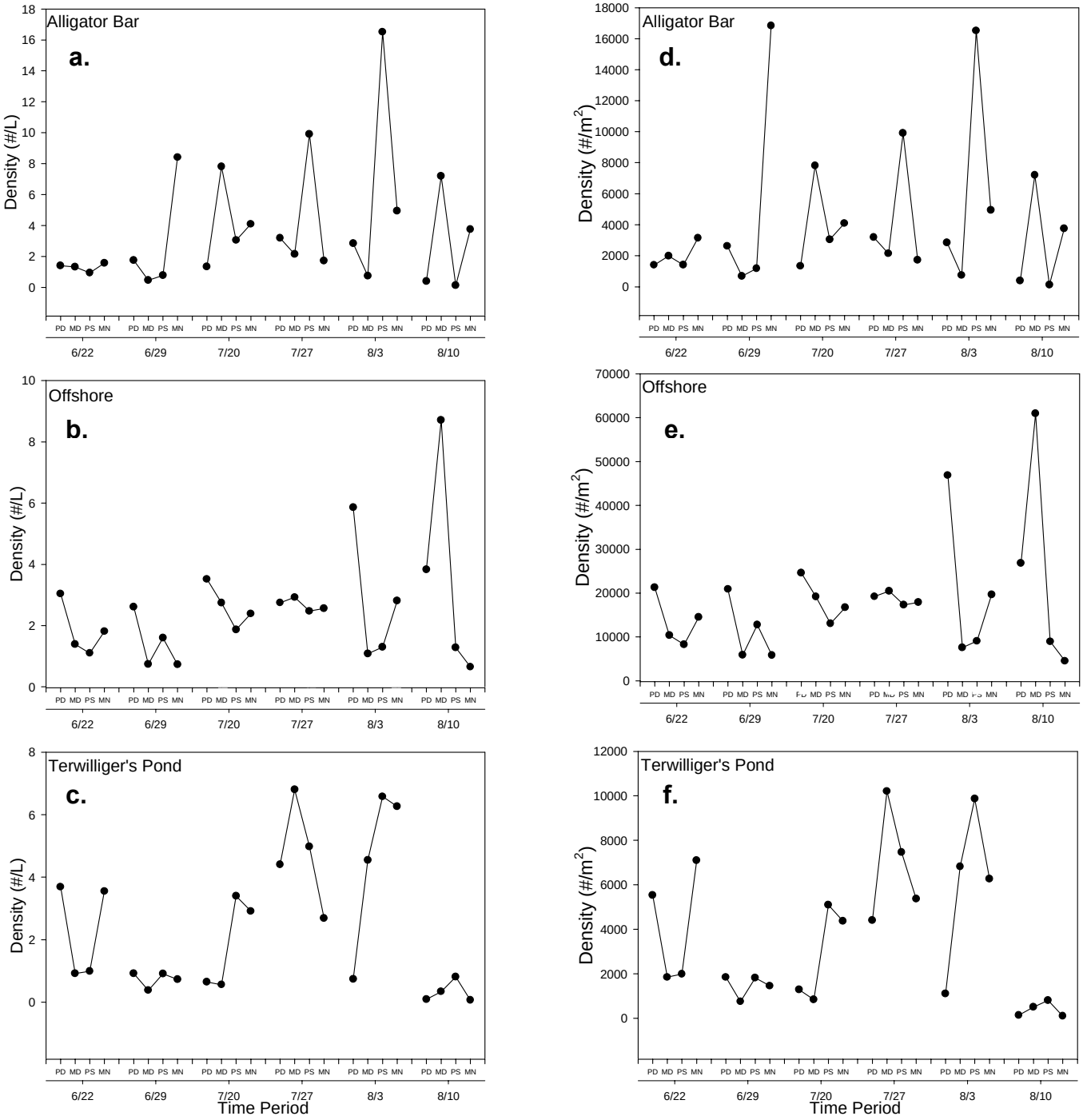

Figure 4- Diel variation in calanoid copepod volumetric density (left) and areal density (right) at the individual dates sampled in Summer 2005 at Alligator Bar (a, d), Offshore (b, e), and Terwilliger's Pond (c, f). PD=Pre-Dawn, MD=Midday, PS=Pre-Sunset, MN=Midnight. Note: the scales are different for each graph panel

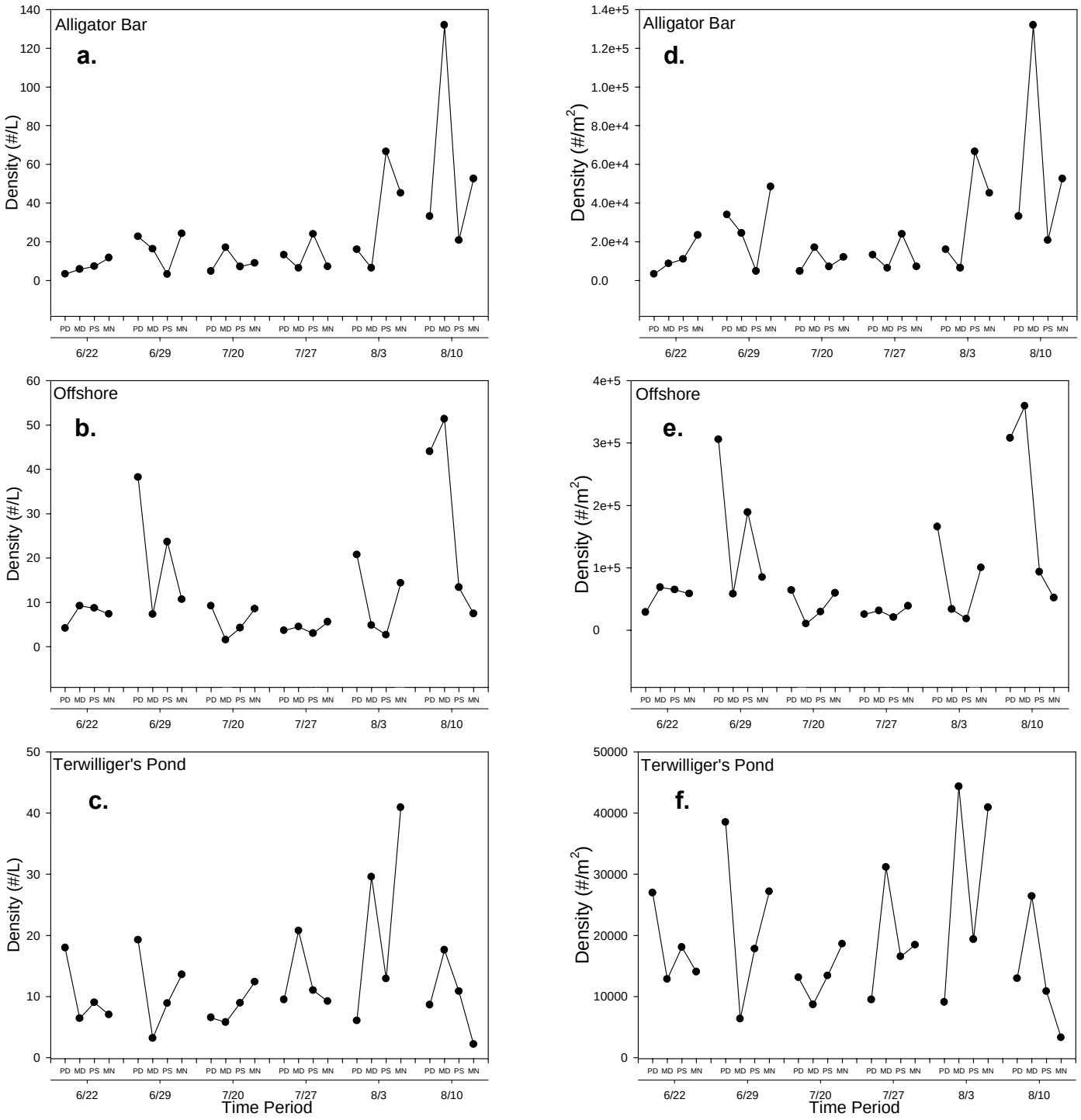

Figure 5- Diel variation in cyclopoid copepod volumetric density (left) and areal density (right) at the individual dates sampled in Summer 2005 at Alligator Bar (a, d), Offshore (b, e), and Terwilliger's Pond (c, f). PD=Pre-Dawn, MD=Midday, PS=Pre-Sunset, MN=Midnight. Note: the scales are different for each graph panel

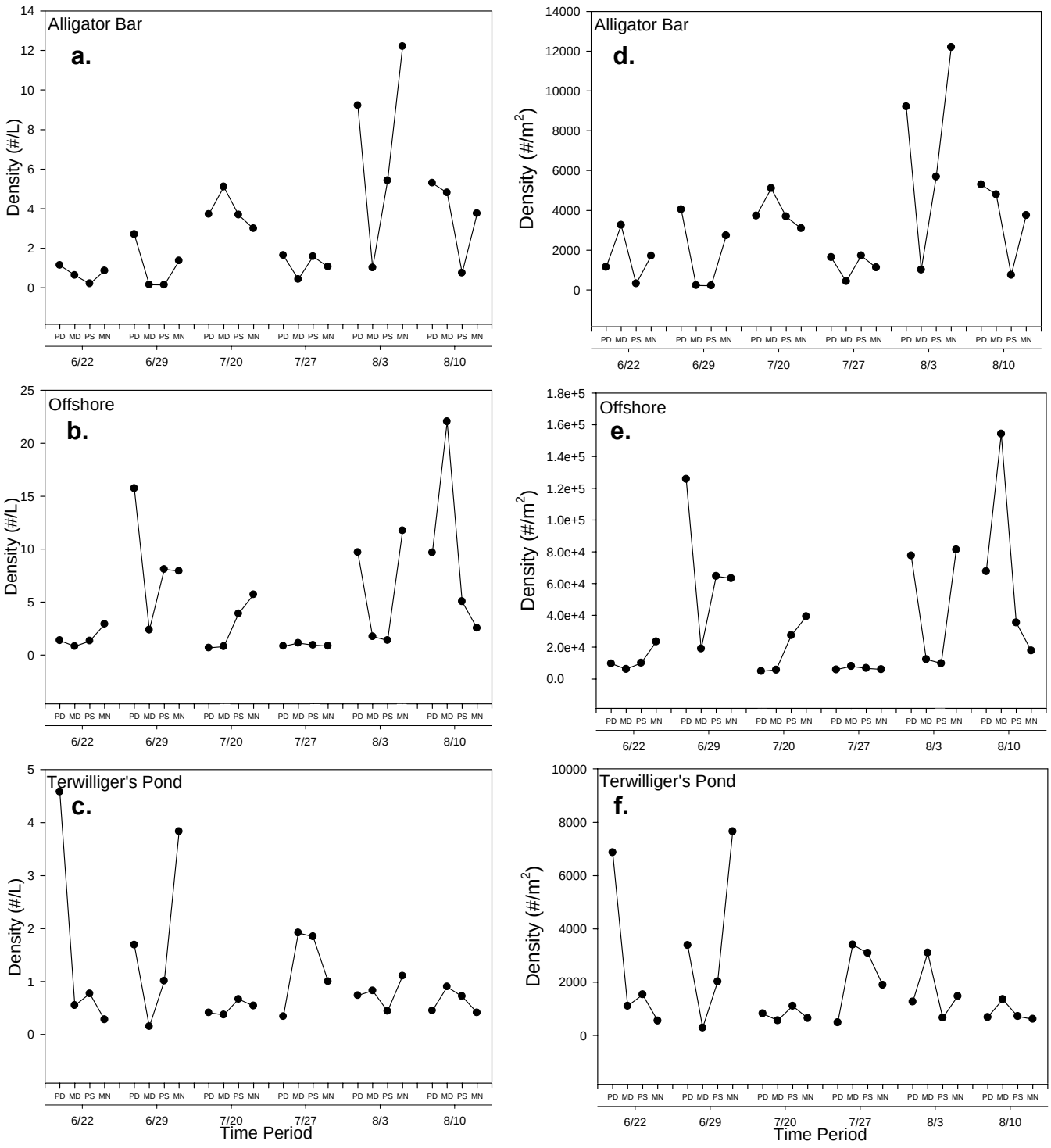

Figure 6- Diel variation in cladoceran volumetric density (left) and areal density (right) at the individual dates sampled in Summer 2005 at Alligator Bar (a, d), Offshore (b, e), and Terwilliger's Pond (c, f). PD=Pre-Dawn, MD=Midday, PS=Pre-Sunset, MN=Midnight. Note: the scales are different for each graph panel

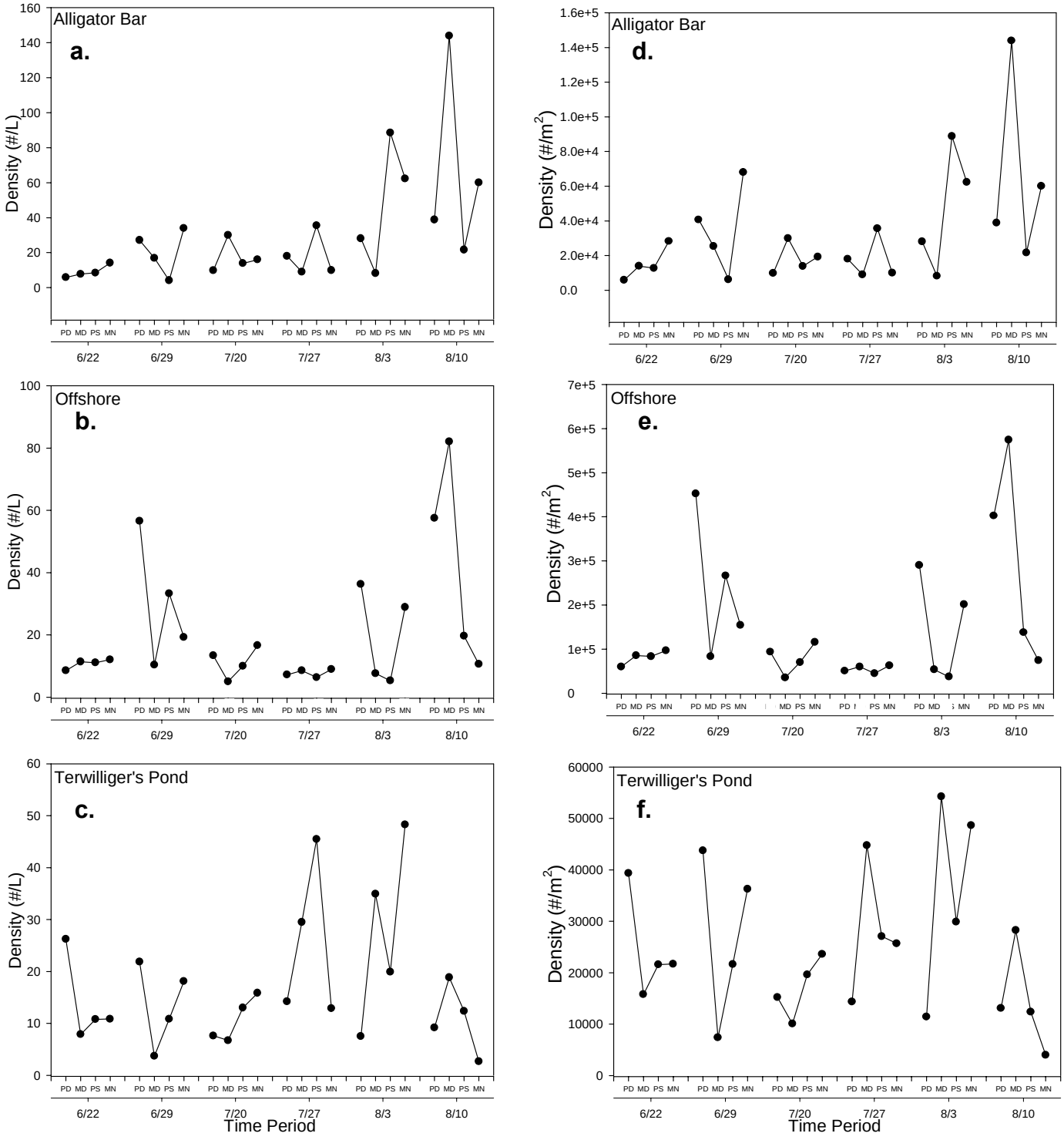

Figure 7- Diel variation in total crustacean zooplankton volumetric density (left) and areal density (right) at the individual dates sampled in Summer 2005 at Alligator Bar (a, d), Offshore (b, e), and Terwilliger's Pond (c, f). PD=Pre-Dawn, MD=Midday, PS=Pre-Sunset, MN=Midnight. Note: the scales are different for each graph panel

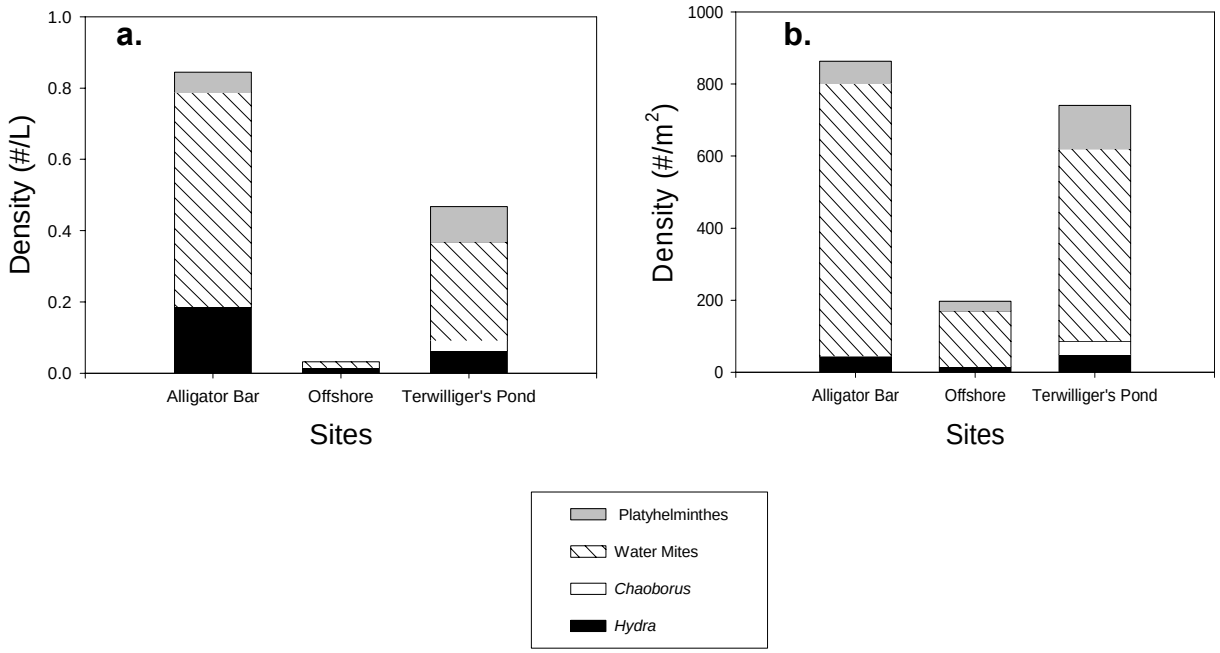

Figure 8- Zooplanktivorous invertebrate volumetric density (a) and areal density (b) at three sites in the western basin of Lake Erie.